COLOR IN OPISTHOBRANCHS

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ABSTRACT

Evidence for the possible functions of color in opisthobranchs is reviewed. There is no evidence for the occurrence of intraspecific color signals, nor for fortuitous colors, so it is probable that all colors function in interspecific contexts, most (or perhaps all) being anti-predatory in function.

There is abundant evidence for crypsis in opisthobranchs and from this certain nudibranchs have evolved precise 'special resemblances' to their food in the form of sponge or coelenterate mimicry. Some can change color to match their food by sequestering pigments from it.

Warning colors and müllerian mimicry probably occur in some opisthobranchs, but evidence for these functions is largely indirect. Colors can also be used in a few species to deceive predators (flash coloration); to intimidate them (deimatic behaviour); or to direct attacks to expendible and/or noxious parts of the body (deflective marks), but experimental studies are lacking. There is tremendous scope for critical experimental studies of color in predator-prey interactions in opisthobranchs.

Typical gastropods have a coiled shell into which the body can be withdrawn when the animal is attacked by a predator. Many predators, however, have evolved ways of overcoming the defensive shell of gastropods, and as a consequence many gastropods have evolved additional anti-predator defensive adaptations, most notably chemical defences (Ansell, 1969; Edmunds, 1974). These chemical defences must have been a preadaptation for the evolution of opisthobranch molluscs which have reduced or even completely lost the shell. In a mollusc that was well protected by means other than the shell, the shell would have been a positive liability for several reasons: it is heavy; it provides anchorage for tube feet of starfish; its formation requires considerable expenditure of energy; it restricts the available position in the body for the gills and for the anal, renal and reproductive openings; it has a characteristic outline that is difficult to conceal; and it constrains the possible evolution of different body shapes and habits. It is no doubt for these reasons that the shell has been reduced and lost independently in the Nudibranchia, Ascoglossa (= Sacoglossa), Aplysiacea and Bullacea. These naked molluscs or sea-slugs have the entire dorsal surface available for the anal, renal and reproductive openings and for gaseous exchange (instead of these being confined to the mantle cavity or lateral mantle groove), and it can also be fashioned into a variety of shapes with firm or flexible processes such that the characteristic outline of the animal is totally obscured. Such processes can be used for respiration, defence, or digestion (by containing within them extensions of the gut). The mantle and its processes can also be protectively colored, and it has long been recognised that protective coloration is widespread in opisthobranchs (Garstang, 1890). Protective coloration in the context of the varied defensive adaptations of nudibranch molluscs has been reviewed by Edmunds (1966a, 1968a, 1974), Harris (1973), Ros (1974, 1976, 1977), Thompson (1976) and Todd (1981). Color, however, can have functions other than protection, and it is necessary to review these possible functions of color in opisthobranchs before assuming that all coloration is necessarily protective.

THE FUNCTIONS OF COLOR IN ANIMALS

The functions of external colors of animals can be considered in three categories:

1. INTERSPECIFIC SIGNALS. Color marks in animals can act as releasers of behavior in other species. Such behavior can be mutualistic as with the cleaner fish whose color signals are recognised by 'customer' fish (Edmunds, 1974), but more usually they function in a defensive context. Aposematic colors warn a predator that an animal is distasteful, and deimatic colors startle a predator (Edmunds, 1974). Cryptic colors by contrast emit signals that are indistinguishable from background noise. They function to reduce the chances of a predator finding an animal. Following Robinson (1969) and Kruuk (1964), Edmunds (1974) distinguished primary

defences, which operate before a predator initiates prey-catching behavior, from secondary defences, which operate when an animal encounters a predator. Primary defences which involve coloration are crypsis, aposematism and batesian mimicry, and secondary defences are flight (flash behavior), deimatic behavior and deflection of an attack (Edmunds, 1974). In this paper these six headings will also be used in examining the defensive behavior of opisthobranchs, but one further heading has been added: special resemblance. Batesian mimics typically resemble active, aposematic animals, but there are also mimics of sessile objects including sticks, leaves and bird-droppings. Edmunds (1974) included these in batesian mimicry, but Vane-Wright (1980, 1981) prefers to regard them as crypsis. This is of relevance in opisthobranchs because some species appear to have very precise resemblances to sponges and coelenterates. The distinction between crypsis and mimicry is discussed by Cloudsley-Thompson (1981), Edmunds (1981a), Endler (1981), Robinson (1981), Rothschild (1981) and Vane-Wright (1981), but here I have evaded the problem by following Cott (1940) and classifying extreme forms of crypsis which resemble specific sessile animals as 'special resemblance'.

2. INTRASPECIFIC SIGNALS. Colors and certain specific behaviors can also act as signals which release a particular behavior in another individual of the same species. Examples are courtship and territorial behavior in many birds and fish such as the stickleback (*Gasterosteus aculeatus* L.), and pecking by herring gull chicks (*Larus argentatus* Pontopidan) at the red spot on the beak of its parent (Tinbergen, 1951). A more unusual example is the dummy eggs on the anal fin of male *Haplochromis burtoni* Günther which stimulate the female to attempt to snap these up into her mouth along with the real eggs. In doing this she engulfs sperm which fertilise her eggs (Wickler, 1968). Signals such as these can only function in animals that have good eyesight.

3. FORTUITOUS COLORS. The colors could be the result of selection pressures quite unrelated to the visual system of any observers of either the same or different species. The pigment deposited in the skin would be the outcome of some biochemical process whose importance was unrelated to the color it produced. Such coloration could be non-adaptive and could actually be to the animal's disadvantage if it is outweighed by the advantage of the associated biochemical process.

This is a difficult hypothesis to prove, but it is possible to test for its occurrence in permanently dark environments where colors cannot possibly have any intra- or inter-specific function. If fortuitous colors occur in these environments we can make two alternative predictions:

1. Each species would evolve a unique coloration either because it retained the adaptive colors of its ancestors from light environments, or because its genes for some specific biochemical process are linked to body color;

2. A group of unrelated species would convergently evolve a particular color because this color is the outcome of some biochemical process of adaptive importance in that environment.

However, if fortuitous colors do not occur then one could predict that in a totally dark environment there would be selective advantage to animals conserving energy by not manufacturing pigment; such white animals would have more energy available for reproduction and could, in the course of time, outreproduce pigmented individuals.

These predictions can be tested in three areas: in the deep sea, in underground caves, and deep in soil, sand or mud. In the deep sea, where there is no or very little light, many animals are red or black (Hardy, 1956). The evidence, however, indicates that in crustaceans and fish these colors are not fortuitous but are adaptations that make the animals cryptic in the dim light descending from above or produced by luminescent animals. In the hadal region where there is no trace of sunlight many fish have reduced eyes but are still pigmented black. This pigment is probably of protective value because there are some fish with luminescent 'searchlight' organs and exceptionally large eyes which would find unpigmented fish more easily (Marshall, 1979). Gastropods from deep sea trenches, however, are often white and lack eyes, so presumably there is no protective advantage for them to have pigment.

In underground caves, there is also perpetual darkness, but animals here totally lack body pigment so are either whitish or transparent. These animals have evolved from normally pigmented ancestors that entered the caves.

In animals that burrow deeply in soil, mud or sand and never come to the surface there would be no advantage in terms of camouflage in having dorsal skin pigment, so we might expect fortuitous colors to occur. *Collembola* living near the soil surface are typically dark brown or grey and so are well camouflaged whenever they are fully exposed, but species that live deeper where there is no trace of light are white and entirely lacking in pigment (Kühnelt, 1961). The available evidence, therefore, does not support the occurrence of fortuitous colors in the deep sea, in caves or in soil and sand, but no critical examination of evidence for fortuitous colors in opisthobranchs has been undertaken.

INTERSPECIFIC SIGNALS

CRYPTIC COLORATION - CAMOUFLAGE

There is a large literature of reports of opisthobranchs being cryptic on their normal background. Very often the normal background is actually their food, as with dorids which feed and rest on sponges. Ros (1976) and Todd (1981) recognise various categories of crypsis based on Cott (1940) and earlier workers, for example homochromy (resemblance of color), homotypy (resemblance of body form), disruptive coloration, countershading and elimination of lateral shadow. Most cryptic opisthobranchs exhibit more than one of these adaptations, but there is practically no evidence to show that any apparently cryptic opisthobranch is less likely to be found and eaten by a predator when camouflaged on its normal background than when relatively conspicuous elsewhere. Cryptic coloration will evolve only if there is selective advantage accruing to cryptic individuals in terms of reduced

detection and killing by predators. Nevertheless, in the absence of such evidence, if we can show that there are elaborate adaptations which improve crypsis to human eyes, then it is reasonable to assume that these adaptations have evolved through predator selection. The survival value of camouflage has been demonstrated many times in other animals such as grasshoppers, mantids and fish (Cott, 1940; Edmunds, 1974).

The dorids *Archidoris pseudoargus* (Rapp) from Europe and *A. montereyensis* (Cooper) from California are mottled yellowish brown and cryptic on their normal food the sponge *Halichondria panicea* (Pallas). The spicular mantle has a similar texture to the sponge so that even when not resting on their food these dorids still resemble sponges. Red dorids of the genus *Rostanga* are similarly found on red sponges, *R. rubra* (Risso) from Europe on *Microciona atrosanguinea* Bowerbank, and *R. pulchra* McFarland from the Pacific on *Oplitaspongia pennata* Lambe (Todd, 1981; Cook, 1962). *R. pulchra* has a clear preference for feeding on *O. pennata* rather than some other sponges, and can detect it chemically from some distance (Cook, 1962). By contrast *A. montereyensis* is unable to orientate in a current towards *H. panicea*. If this difference in chemosensory ability occurs also in European species of these genera it would explain why *R. rubra* is usually found close to red sponges while *A. pseudoargus* is very often found some distance from its food (personal observation).

Jorunna tomentosa (Cuvier) also feeds on *Halichondria panicea* (Todd, 1981). It not only resembles its food in color and texture, but its rhinophoral openings and the way the gills are held in an erect circlet closely mimic the openings of the sponge (personal observation). *Aldisa banyulensis* Pruvot-Fol is another red dorid that feeds on sponges, and in addition to color resemblance, it has two depressions on the mantle that resemble sponge oscula. The yellow dendrodorid *Doriopsilla pharpa* Marcus is also highly cryptic on its food sponge *Cliona celata* Grant; the population dynamics of this association have been studied by Eyster and Stancyk (1981). In summary, many, perhaps the majority, of spiculose dorids belonging to the family Dorididae *sensu lato* (including the genera *Doris, Archidoris, Anisodoris, Discodoris, Atagema, Rostanga, Aldisa*) as well as many porostomatous Dendrodorididae (*Doriopsilla, Dendrodoris*) are cryptic in both color and form when in their normal environment amongst their sponge food.

Many eolid nudibranchs are also cryptic when on their hydroid foods for example the brownish *Cuthona amoena* (Alder and Hancock) and *Cuthona concinna* (Alder and Hancock) (Thompson and Brown, 1984). *Cuthona foliata* (Forbes and Goodsir) has conspicuous orange marks, but it is also cryptic amongst hydroids, perhaps because these colors are disruptive marks (Todd, 1981). *Eubranchus exiguus* (Alder and Hancock) and *Tergipes tergipes* (Forskål) are both small animals with mottled patterns of brown, olive and white. They also have large, swollen cerata which resemble the polyps and thecae of calyptoblast hydroids (Giard, 1888). *T. tergipes* has few cerata, and these alternate to left and right, so that it bears a very close resemblance to *Obelia* and

Laomedea spp. *Catriona gymnota* (Couthouy), several species of *Coryphella*, and *Facelina coronata* (Forbes and Goodsir) all have red diverticula in the cerata and are beautifully camouflaged on their normal food *Tubularia* spp. (Giard, 1888; Todd, 1981). Some species are very restricted in the foods they will eat: *C. gymnota* is very rarely found eating any hydroid other than *Tubularia* (except possibly when newly metamorphosed, see Todd, 1981), and in choice experiments has a specific preference for it (Braams and Geelen, 1953). *Cuthona nana* (Alder and Hancock), another species with pink in the cerata, is virtually confined to a single prey species, the pink *Hydractinia echinata* Fleming which normally lives only on hermit crab shells (Harris et al., 1975; Rivest, 1978). *Dondice paguerensis* Brandon and Cutress is a brownish eolid that is also camouflaged on its prey, the scyphozoans *Cassiopea xamachana* Bigelow and *C. frondoza* Fuwkes (Brandon and Cutress, 1985). A more aberrant eolid, *Glaucus atlanticus* (Forster), has remarkably elongated cerata, probably as an adaptation to buoyancy, and is camouflaged as it floats alongside its blue food, the chondrophores *Velella* and *Porpita* (Thompson and McFarlane, 1967; Thompson and Bennett, 1970). Its upper (ventral) surface is blue while its lower (dorsal) surface is white, so it has reversed countershading (Todd, 1981) like hawkmoth caterpillars (Cott, 1940).

Camouflage occurs in many other opisthobranchs. Most Ascoglossa (= Sacoglossa) are green due to symbiotic photosynthetic plastids which they sequester from their algal food, but *Elysia arena* Carlson and Hoff from the Pacific lives on sand at the base of its food (*Caulerpa* spp.), and instead of being green it is orange-brown (Carlson and Hoff, 1977). Similarly many species of *Aplysia, Bursatella* and *Dolabrifera* are brownish and camouflaged on their brown algal food or on sublittoral rocks. However, *Phyllaplysia zostericola* McCauley lives on the leaves of eel grass (*Zostera marina* L.) where its flattened form, green color and longitudinal white lines resembling veins give it near perfect camouflage (McCauley, 1960).

Cryptic coloration will reduce the chances of a predator finding an animal so long as the animal rests on a background of the appropriate color. Opisthobranchs, however, probably lack color vision and are slow moving, so they could be unable to select an appropriate colored resting place visually. Instead, background color-matching is achieved by sequestering pigment from their food. Abeloos and Abeloos (1932) found that two pigments in *Archidoris pseudoargus* and its food *Halichondria panicea* are identical. While blue pigment was confined to the digestive gland of the nudibranch, yellow carotenoid is found extensively in body tissues and so contributes to the external coloration. Similarly the pink dorid *Hopkinsia rosacea* MacFarland sequesters a pink xanthophyll from its food the bryozoan *Eurystomella bilabiata* Hincks (Strain, 1949; McBeth, 1971). Harris (1973) summarises similar work on other Pacific dorids by Coulom, Anderson and McBeth. The carotenoids that contribute to the red of *Rostanga pulchra* are obtained from its food, but the particular carotenoids present depend on which species of sponge it has recently been eating.

Many species of *Aplysia* change diet and color as they

grow, for example *A. parvula* Guilding, when young, is pink and feeds on the pink alga *Asparagopsis taxiformis* (Del.) Trev., but as it grows it migrates to the greenish *Laurencia johnstonii* and it too becomes greenish (Faulkner and Ghiselin, 1983). However, it has not been confirmed that this is due to a direct sequestration of pigment from the food although this is probable. In the Ascoglossa that have symbiotic algae, these are acquired by ingestion and stored in the body tissues so contributing to the animals cryptic color when resting on green algae (Clark and Busacca, 1978; Jensen, 1980).

Background color-matching by acquiring pigment from food works well with species with restricted diets (stenophagy). Euryphagous species (with a wide range of foods) can often change color according to diet. Labbé (1931) reports that *Aeolidiella glauca* (Alder and Hancock) and *Favorinus branchialis* (Rathke) with white digestive glands in the cerata became red after feeding for a day on sea anemones (*Actinia equina* L. and *Anemonia sulcata* Pennant). Tardy (1969) reports that *Aeolidiella sanguinea* (Norman) can be red or brown depending on diet. Haefelfinger (1969) was also able to change the ceratal color of *Spurilla neapolitana* (delle Chiaje) by feeding them with different sea anemones, while Edmunds (1983) observed that pale grey *Aeolidia papillosa* (L.) fed on red *Actinia equina* developed red digestive glands in the cerata. In this way an eolid that moves to a new food quickly acquires the same color as this food and so becomes cryptic. Many eolids can change color in this way, but the range of colors they can acquire varies in different species. The ceratal digestive gland of *Phestilla lugubris* Bergh (= *P. sibogae* Bergh) takes on the color of the part of the coral it has been eating, so it is camouflaged yellow or brown (Harris, 1971a). The closely related *P. melanobrachia* Bergh, however, can develop a much wider range of colors (Harris, 1968, 1971a, b, 1973). *P. melanobrachia* sequesters four of its five types of pigment from the various species of coral it eats. First, red, pink, orange, yellow and black pigments similar to flavones are stored in the digestive gland and can be quickly lost and acquired as an eolid moves from one species of coral to another. A granular black pigment that also accumulates in the digestive gland, and a red carotenoid pigment that is deposited in the epidermis are also obtained from the food but are permanent. Finally, specimens that have fed on the coral *Turbinaria* spp. sequester zooxanthellae in the digestive gland which makes them dark grey. The result of this complex treatment of food pigments is that 95% of *P. melanobrachia* found in the sea on their coral food were cryptic, but a few which had recently moved or had acquired permanent pigments were conspicuous.

Because an eolid that moves on to a new species of food is likely to be conspicuous for a few days one could expect that many eolids could be found that have not had time to adapt to their new diet and so are conspicuous. One reason why so few conspicuous eolids are found is probably because of ingestive conditioning: Hall et al. (1982) found that *Aeolidia papillosa* that had been fed on *Sagartia troglodytes* (Price) had a preference for this species of sea anemone when given a choice, but if the same animals were kept on *Actinia*

equina they quickly acquired a preference for this anemone over *Sagartia*. Hence an *A. papillosa* that has fed on *Actinia equina*, and has acquired red cerata which make it cryptic on this anemone, will tend to continue feeding on *Actinia equina* even if other anemones are nearby (Edmunds, 1983). Ingestive conditioning also provides a simple explanation for the different food preferences found in experiments on this eolid by various workers (Stehouwer, 1952; Waters, 1973; Harris, 1973; Edmunds et al., 1974; Tardy and Bordes, 1978).

A further way in which opisthobranchs can change color is by differential expansion and contraction of chromatophores. This is the normal method of color change found in fish, reptiles and cephalopods, but it has only been demonstrated in one species of opisthobranch, the shallow-burrowing bullacean *Haminoea navicula* (da Costa) (Edlinger, 1982). When placed on a dark background the dark chromatophores expand over a period of a week to make the animal largely black, while on a pale background they retract so that the animal becomes very pale. This change is presumably mediated through the eyes. Since the change results in color matching of the animal to its background it is reasonable to assume that it has evolved through predator selection for camouflage.

SPECIAL RESEMBLANCE

In some nudibranchs the cryptic adaptations extend beyond coloration and superficial texture (e.g. spicules in dorids) to precise similarities of body form to that of the food. This is special resemblance. Whether special resemblance should be regarded as a form of crypsis or mimicry is a matter of definitions (Vane-Wright, 1980; Edmunds, 1981a), though Robinson (1981) argues that if the animal resembles its model even when separated from it then this should be regarded as mimicry. Some of the examples already mentioned approach this category, for example *Jorunna tomentosa* which has openings dorsally that resemble sponge oscula, and *Catriona gymnota* whose oval red cerata resemble the gonophores of *Tubularia* (personal observation).

Corambid dorids are circular, flattened and lacking a dorsal crown of gills. Their diet appears to be confined to bryozoans, especially *Membranipora*. When resting or feeding on *Membranipora* they are extremely difficult to detect because a cellular pattern on the mantle resembles the bryozoan zooids. Observations on the ecology of *Doridella steinbergae* (Lance) on *Membranipora* spp. growing on *Laminaria saccharina* (L.) at Friday Harbor have been described by McBeth (1968) and Seed (1976), while similar observations have been made on *Doridella obscura* Verrill by Franz (1967) in the west Atlantic. Perron and Turner (1977) have shown that veligers of this latter species can be induced to metamorphose by the presence of its normal food *Electra* (= *Membranipora*) *crustulenta* (Pallas) but not by three other species of bryozoan.

Aegires sublaevis Odhner is another dorid with a special resemblance in color, shape and texture to its food, the sponge *Clathrina coriacea* (Montagu) (Ros, 1976, 1977). Another nudibranch, *Tritonia nilsodhneri* Marcus, lives on the gorgonian *Eunicella verrucosa* (Pallas) which can be pink or white. The nudibranch matches its food in color as well as

form with its branched gills resembling the gorgonian polyps (Tardy, 1963; Thompson and Brown, 1984; Just and Edmunds, 1985).

A group of species of nudibranchs that live exclusively on corals has recently been extensively studied. The eolids *Phestilla melanobrachia* and *P. lugubris* are both camouflaged on their normal food coral (Harris, 1968, 1971, 1973). They hold their cerata laterally instead of dorsally so they are inconspicuous when resting on their coral food, but there is no close 'special resemblance' to the host. *P. minor* Rudman, however, has a brown mottled form that is very well camouflaged on the scleractinian coral *Porites somaliensis* Gravier, as well as a white form that matches fish feeding-scars and patches of white coral sand on the *Porites* (Rudman, 1981a). *Cuthona poritophages* Rudman is another eolid that lives only on *P. somaliensis* (Rudman, 1979). It is beautifully camouflaged in color, shape and lateral position of its cerata when the coral polyps are expanded, but is more conspicuous when the polyps are retracted. The aberrant nudibranch *Pinufius rebus* Marcus and Marcus, however, is not merely camouflaged on *Porites somaliensis*, but, like corambids on bryozoans, it closely resembles its food in body form and color markings (Rudman, 1981a). Ridges on its back resemble the edges of individual polyps, white-tipped tubercles occur on both the retracted polyps and on the dorsum of the nudibranch, and there are white-tipped cerata of similar color, size and shape to the coral tentacles.

Just as species of *Phestilla* are associated with scleractinian corals, so species of the eolid genus *Phyllodesmium* appear to be associated with alcyonarians. Some appear to have simple camouflage, but in others the resemblance to a specific alcyonarian extends to color, shape of body and shape of cerata (Rudman, 1981b). *P. poindimiei* (Risbec) bears a very close resemblance to its food, the orange soft coral *Telesto* sp., *P. hyalinum* Ehrenberg has an even more perfect resemblance to a yellowish species of *Xenia,* and *P. cryptica* Rudman has yellowish or bluish knobbed cerata exactly matching the color and knobbed tentacles of the various forms of *Xenia* on which it lives. Species of the aeolidiid genus *Aeolidiopsis* also feed and have a specific resemblance to their food, the colonial zoantharian *Palythoa* spp., while the aberrant, flattened arminacean *Doridomorpha gardineri* Eliot is quite remarkably camouflaged on the coral *Heliopora* sp. (Rudman, 1982a). However, by far the most extreme adaptation in terms of mimicry of a specific food is that of the eolid *Cuthona kuiteri* Rudman from Australia whose cerata have tiers of tentacles closely resembling the tentacles of the aberrant hydroid *Zyzzyzus spongicola* (von Lendenfeld) whose polyps project from sponges (Rudman, 1981c).

Although *Cuthona kuiteri* is clearly a hydroid mimic with a 'special resemblance' to *Zyzzyzus*, it is not easy to decide whether some of the other nudibranchs are simply cryptic or have a special resemblance. The distinction is in terms of predator perception: if predators overlook a nudibranch because it merges with its background, then the nudibranch is cryptic; but if predators ignore it because they mistake it for a coelenterate they do not eat, then the nudibranch has a special resemblance to the coelenterate.

APOSEMATIC (WARNING) COLORATION

A number of species of opisthobranch mollusc are highly colored and conspicuous in their natural environment and it has been suggested that the following have warning coloration: *Limacia clavigera* (Müller), *Polycera quadrilineata* (Müller), *Eubranchus tricolor* Forbes, *Facelina coronata* (Forbes and Goodsir) (Hecht, 1896); species of Chromodorididae including *Chromodoris reticulata* (Pease) and *C. diardii* (Kelaart) (Crossland, 1911); and many eolids (Garstang, 1889; Herdman, 1890; Herdman and Clubb, 1890). Garstang (1890) and Hecht (1896) were, however, well aware that not every brightly colored nudibranch is necessarily aposematic, and they pointed out that some are actually cryptic in their normal environment; but they both believed that some species are conspicuous and do have warning colors. More recently Ros (1974) has drawn attention to groups of brightly colored aposematic species of chromodorid, while Harris (1973) and Todd (1981) mention species that are also probably aposematic such as the tropical *Phyllidia varicosa* Lamarck and the West Pacific *Triopha carpenteri* Stearns and *Diaulula sandiegensis* (Cooper). Thompson (1960) cautioned against the simplistic view that cryptic species are palatable while aposematic ones are not, and Edmunds (1974) argued for more experimental evidence before one should conclude that aposematic coloration really does occur in opisthobranchs.

A recent definition of aposematism has been given by Edmunds (1974): "Animals which have dangerous or unpleasant attributes, and which advertise this fact by means of characteristic structures, colours, or other signals so that some predators avoid attacking them, are said to be *aposematic*, and the phenomenon is called *aposematism*".

If this definition is accepted then in order to demonstrate aposematic coloration it is necessary to establish:

1. that a species is conspicuously colored or advertises itself in some other way;

2. that it is sufficiently noxious that some predators will not eat it;

3. that some predators avoid attacking it because of its color (or other signal);

4. that this color or other signal provides better protection to the individual or to its genes than would other (e.g. cryptic) signals.

Only if all four of these criteria are met will there be selective advantage in the warning signals. If criterion 4 is not met then there can be no advantage in an animal being conspicuous: it would be better protected if it were cryptic and warning colors could not evolve. Criterion 1 is well documented (see above). Criterion 2 is also well established; Crossland (1911), Crozier (1916) and Thompson (1960) have all demonstrated that a variety of species of brightly colored nudibranchs are unpalatable to fish. The molluscs were usually dropped into aquaria or the sea whereupon fish attacked them as they fell through the water. Almost every mollusc, however, survived even though it may have been ingested and spat out several times before reaching the substrate, after which it was usually ignored. Criterion 3 was not established in these experiments, perhaps because the stimulus to snap at any potential food

object falling through the water is so powerful that it overrides any possible learned aversive response (Edmunds, 1974). Most shallow-water fish have color vision and are capable of learned responses, but so far only very preliminary experiments have been carried out to test if fish can learn not to attack nudibranchs that they have, a few minutes earlier, found to be distasteful (Edmunds, 1974). Nevertheless, since birds, amphibians, reptiles and octopus can quickly learn to avoid conspicuous but noxious prey it is probable that fish can do so as well (evidence summarized in Edmunds, 1974). Criterion 4 has not been demonstrated in any marine predator.

Predators can acquire an aversive response to aposematic prey in two distinct ways: first, by learning (negative conditioning); and second, by a long period of exposure to noxious prey over many generations during which they evolve an innate aversive response to certain specific signals (see e.g. Smith, 1975, 1977).

It is reasonable to conclude that aposematic coloration probably does occur in many nudibranchs, although it remains unproven. The species in which it is most likely to occur are the chromodorids, phyllidiids and perhaps some eolids. There is some indirect evidence that supports this conclusion. Where aposematism occurs and where the relevant predators have to learn by experience to avoid the warning colors, then it will pay the various aposematic species to evolve similar color signals (müllerian mimicry). In this way predators will have to sample (and perhaps kill) a much smaller number of individuals before they have established their conditioned avoidance response than if there were several different color signals, and the loss to prey while they learn will be spread among several species. Examples of nudibranchs that are not closely related taxonomically but which share a common pattern have been documented by Ros (1974, 1977). Details are given below, but the occurrence of what appears to be müllerian mimicry supports the hypothesis that these animals have warning colors.

Another possible example of warning coloration is described by Thompson (1985). He reports that the dorid *Peltodoris atromaculata* Bergh and the pleurobranchid *Berthella stellata* (Risso) are both conspicuous to divers in the Mediterranean, and that they are very variable in the pattern of dark and white markings. If warning coloration occurs one can predict that the pattern should be relatively constant in any one population since then predators need only learn one pattern in order to avoid all individuals. If the population is variable, or polymorphic, then predators might have to learn several patterns, and hence would sample many more individuals before they could learn to avoid them all. This argument supports the view of Ros (1976) that *P. atromaculata* is actually cryptic with disruptive coloration and is not conspicuous. Clearly, as Thompson (1985) indicates in his note, more information is required on the variation in these species both within and between populations. Perhaps they are monomorphic and aposematic in some populations but polymorphic and cryptic in others depending on the predators in each locality.

Another problematical example is the eolid *Eubranchus farrani* (Alder and Hancock). This species is typically brilliant orange-yellow and white and so is relatively conspicuous on the dull colored hydroids which it eats. However, Edmunds and Kress (1969) showed that the population at Plymouth is polymorphic with four color forms: orange and white; orange; orange and brown; and white. There may be additional color morphs elsewhere (Thompson and Brown, 1984; Just and Edmunds, 1985). Once again, it is difficult to explain the occurrence of so many color morphs if the colors are aposematic, and one almost begins to take seriously the view of Crozier (1916), based on *Hypselodoris zebra* Heilprin, that the color is fortuitous and the result of selection pressures for some other character that just happens to be associated with color.

There are, however, several possible explanations of color variation in *Eubranchus farrani*. For example, the different frequencies of the various morphs in different populations could reflect different species of predators. It could be that the typical orange-yellow and white form is selected for in areas where predators quickly learn to avoid this pattern either by attacking and rejecting *E. farrani* or by attacking a similarly colored species such as *Polycera quadrilineata*. In areas where it is rare and where no müllerian mimics occur, or where the relevant predators fail to learn not to attack it, it could be more advantageous to be cryptic (dark brown for example). There could also be areas where it pays to have several color morphs because predators could be hesitant to attack novel prey. This is apostatic selection but it is more likely to occur in cryptic than in aposematic animals (Clarke, 1962; Edmunds, 1974).

A third problem is posed by brilliantly colored but rare species. *Polycera elegans* (Bergh) is orange with blue spots and was found only six times in 66 years (Edmunds, 1961) despite being large and very conspicuous. It has been found more frequently in recent years by divers, but it remains a local and uncommon species except at Lundy where it is sometimes abundant (Thompson and Brown, 1984). The problem is how a scarce species can benefit by evolving warning colors. Because it is rare, predators are unlikely to evolve an innate aversive response, so they must learn by experience to avoid it. But the experience of a predator sampling a noxious prey can be fatal to the prey even if it is eventually rejected by the predator. For such prey animals warning colors will only benefit other individuals than the one sampled, and so aposematism can only evolve through kin selection (Harvey *et al.*, 1982). This is unlikely to occur in rare species: it would pay them to be cryptic as this would reduce the numbers killed while the predators learn, and it could not occur in species with planktotrophic larvae since the individuals benefitting from a predator's learned aversion would not necessarily be genetically related to the individual that died. An alternative explanation is that rare aposematic species are tough enough to survive sampling by a predator, so that the individual that is attacked is the one that benefits from the predator's learned aversion (Jarvi *et al.*, 1981; Wiklund and Jarvi, 1982).

BATESIAN AND MÜLLERIAN MIMICRY

Ros (1976, 1977) has suggested five groups of mimetic

nudibranchs which he terms aposematic or mimetic circles. The mimicry could be either batesian or müllerian. In batesian mimicry one or more palatable species mimic an aposematic 'model', whereas in müllerian mimicry several aposematic species share the same color pattern. Ros's first mimetic group are blue and gold chromodorids in which the mantle is largely bright blue with orange, yellow or white markings. In the Mediterranean this group includes *Hypselodoris gracilis* (Rapp), *Mexichromis tricolor* (Cantraine), *H. messinensis* (von Ihering), *Chromodoris krohni* (Verany), *H. valenciennesi* (Cantraine) and *H. bilineata* (Pruvot-Fol). Some of these species occur also on the Atlantic coast of Africa and the Bay of Biscay where additional blue chromodorids include *H. tema* Edmunds from Ghana, *H. cantabrica* Bouchet and Ortea from Biscay and *H. webbi* (d'Orbigny) from the Canaries (Bouchet and Ortea, 1980; Edmunds, 1981b). Chromodorids are well known to be unpalatable to many fish (Crossland, 1911; Crozier, 1916) due to a variety of chemicals (summarized by Schulte and Scheuer, 1982; Thompson *et al.,* 1982; and Faulkner and Ghiselin, 1983), and they have large glands that characteristically exude a secretion when they are attacked (Edmunds, 1981b; Rudman, 1984). Some of these species could simply have evolved from a similarly blue and gold species in the recent past and so their colors are still very similar, but others belong to different genera and are likely to be the result of convergent evolution. Young *H. bilineata,* young *H. gracilis* and adult *M. tricolor* for example have almost identical patterns (Haefelfinger, 1959; Edmunds, 1981b). Rudman (1982b, 1983, 1985, 1986) has described several other similar groups of chromodorids which have evolved similar patterns convergently.

Another mimetic group described by Ros (1976, 1977) is of white nudibranchs with red, orange or yellow markings: *Chromodoris elegantula* Philippi and *Diaphorodoris papillata* Portmann and Sandmeier have red spots and a yellow border; *Crimora papillata* Alder and Hancock, *Ancula gibbosa* (Risso), *Trapania maculata* Haefelfinger, *Polycera quadrilineata* and *Limacia clavigera* have orange or orange-yellow spots or papillae, and *Calmella cavolinii* Verany has red papillae. To these can be added the eolid *Eubranchus farrani* with orange spots, and, in northern Europe, *Polycera faeroensis* Lemche with yellow spots. Ros suggests that this group have evolved towards a well protected eolid such as *Calmella cavolinii* and so presumably some are batesian and some müllerian in their relationship. However, there is no evidence that eolids are any more noxious than the dorids in this group, many of which have defensive glands in dorsal papillae. It is therefore possible that this is another müllerian mimetic group of species, although whether predators can generalise across the entire group, or whether they recognise *Chromodoris elegantula* and *D. papillata* as one type of noxious prey and the remaining dorids as another is not known.

Conclusions on the nature of these mimetic groups must be tentative since there is no information on likely predators and how these perceive nudibranchs, but the fact that such groups exist implies selection for similar color patterns and hence mimicry. Most species are probably müllerian mimics, but some could be batesian, and some could be batesian with respect to one predator but müllerian to another.

FLIGHT AND FLASH COLORATION

Some terrestrial animals increase their chances of escaping by means of flash colors (Cott, 1940; Edmunds, 1974). Although experimental proof is lacking, it is thought that predators pursue a conspicuous color on the fleeing prey, but when the prey stops and conceals this 'flash' color, the predator is left baffled, and could give up the search.

Apart from the Pteropoda (which have not been included in this review) the majority of opisthobranchs are slow moving benthic animals, quite incapable of rapid escape movements. Even species that swim do so comparatively slowly (Farmer, 1970; Thompson, 1976), but this can be sufficient to enable them to escape from slow moving predators. *Tritonia diomedea* swims in response to chemicals released by the starfish *Pycnopodia helianthoides* (Willows, 1967), and several other nudibranchs respond to rough handling by swimming (summarized by Thompson, 1976).

There is one nudibranch which possibly has flash coloration: the Indo-Pacific dorid *Hexabranchus sanguineus* Rüppell and Leuckart. As *Hexabranchus* swims it exposes bright red and white spots on its dorsal surface, but when it comes to rest the edge of the mantle is rolled up, concealing these markings, and the mollusc is then very often cryptic (Edmunds, 1968b). However, there is no published record of a predator pursuing swimming *Hexabranchus*, let alone being confused by its color marks vanishing when it stops swimming.

DEIMATIC BEHAVIOR

Deimatic or frightening behavior is a display that intimidates a threatening predator causing it to hesitate or back away (Edmunds, 1974). Some deimatic behaviors are genuine warnings that an animal is noxious, so they reinforce the primary aposematic defence (as with the skunk *Spilogale putorius*), but others are bluff (e.g. the eyespots of the hawkmoth *Smerinthus ocellatus*). There are several possible examples of deimatic behavior in opisthobranchs. It is well known that when eolids are molested most species contract the rhinophores and extend and wave the cerata vigorously (see e.g. Edmunds, 1966a). Eolid cerata are often brightly colored and this adds to the conspicuousness of the display. Janolids and stiligerid ascoglossans have similar behavior (personal observation). Another example of deimatic behaviour is in *Hexabranchus sanguineus* (= *H. marginatus*) (Edmunds, 1968b, 1974). The crawling animal is cryptic on many parts of the coral reef, but when attacked it responds by unrolling its dorso-lateral mantle thereby exposing bright red and white marks. After a few seconds the mantle margin is rolled up and the mollusc again becomes cryptic. Some chromodorids with wide, folded mantles can have similar behavior although these have not been carefully studied.

Lobiger souverbiei Fischer and *L. viridis* Pease can also show deimatic behaviour (K.B. Clark and R.C. Willan,

respectively, pers. comm). These ascoglossans have four erect flaps on the body which can be autotomised but which are normally held curled over the dorsal surface. When the animal is disturbed, these are unfurled to display vivid red spots on their inner, upper surfaces. After one to two seconds L. viridis refolds the flaps and the spots disappear. Species of Plocamophorus (Polyceridae) have knobbed protuberances (globes) on the body. In P. imperialis Angas these globes are reported to emit a luminous fluid when the animal is molested (Willan and Coleman, 1984).

Although all of these examples appear to be deimatic, in no case has the behavior actually been shown to intimidate predators.

DEFLECTION OF AN ATTACK

Some animals have behavior that diverts predators away from themselves or their young, or they can have deflection marks that direct attacks to either an expendable or a noxious part of the body (Edmunds, 1974). Eolids, some dorids, arminids, dendronotids and ascoglossans have ceratal papillae which they often wave conspicuously when attacked, and which can be autotomised and later regenerated. The cerata are often brightly colored and so a predator which attacks is likely to get a mouthful of these while the nudibranch crawls away unharmed. The cerata also contain defensive structures concentrated near their tips: nematocysts in eolids and glands containing toxic secretions in some eolids, dorids, arminids, dendronotids and ascoglossans (Edmunds, 1966a, b, 1974; Ros, 1976; Harris, 1973; Jenson, 1984). Again, there is no proof that colored cerata function in this way, but by analogy with deflection marks in other animals, it is probable.

INTRASPECIFIC SIGNALS

If visual stimuli play a part in intraspecific behavioral interactions of opisthobranchs, then these molluscs must have good eyes. However, opisthobranch eyes are so simple in structure (summarised in Hyman, 1967; Franc, 1968) that it is virtually certain that they are unable to form an image of, for example, the color pattern of another individual. Hence there is no evidence that colors in opisthobranchs have an intraspecific signalling function.

FORTUITOUS COLORS

Among opisthobranchs there are a few deep sea species but there is very little information on their color in life. Most published accounts are of animals collected on a deep sea expedition when no notes of the living animals were made. The preserved specimens usually lack pigment but it is not known if this is because they were white or because the original pigment has dissolved out. Nevertheless, a careful search of the literature does suggest that opisthobranchs from abyssal depths lack pigment. Bouchet (1975) refers to the color of 14 out of 30 species of abyssal Atlantic opisthobranchs, and the color of two of the remaining 16 is known from other sources. Out of 10 species dredged from depths exceeding 1175 m, eight had white shells and two yellow

shells. Of six species from shallower areas, 140-1080 m, three were white, one yellow, one red, and one white with darker dots [Philine scabra (Müller)]. The red species, Gastropteron rubrum (Rafinesque), and Philine scabra also occur in much shallower water where their color is likely to be visible, and G. rubrum also swims in shallow water (Haefelfinger and Kress, 1967). These data suggest that shallow water benthic species are more often pigmented than abyssal species, though it is far from conclusive. Bouchet (1977) describes a further 16 species of deep sea opisthobranchs: five are variously colored (red, violet, brown, olive, and black spotted) but the rest are uniformly either white or yellow. The colors could be fortuitous, or they could have a function in shallower water as with G. rubrum, but more information is required on their depth range. Another pointer is given by Marcus and Marcus (1969). They describe two species of Philine with brown body color, P. lima (Brown) and P. thurmanni Marcus and Marcus. P. lima was collected from 200 m, but it occurs elsewhere in only 4 m of water, so if it is ever exposed on the surface of the sea bed its brown color could provide camouflage. P. thurmanni occurs from 70 to 4116 m and can be either white or brown. Most of the brown ones were from shallower depths whereas all four white ones came from depths exceeding 4000 m. The authors suggest that the difference in color can be due to different preservatives, but I suggest that it is more likely that the brown is of selective advantage in regions where light penetrates to the sea bed, but white is favored by selection at greater depths.

Animals that show adaptations to cave life are typically freshwater or terrestrial, and no opisthobranchs are known that live only in caves. [Discodoris cavernae Starmühlner, a brown dorid described by Starmühlner (1955) from caves near Naples, is considered by Schmekel and Portmann (1982) to be conspecific with the much more widely distributed D. indecora Bergh despite some unusual features in its reproductive system.]

There are, however, a substantial number of burrowing opisthobranchs, particularly in the Bullacea. These glide through sand or mud using the front part of the body as a plough, and with a copious supply of mucous carrying particles of sand back over the body surface. Many of these animals burrow close below the surface and their dorsal mantle is frequently visible above the sand, so there could still be an advantage in having pigmentation dorsally for camouflage as a defence against predators. Other species burrow more deeply and only rarely come to the surface, and we might predict that in these animals energy saving considerations should lead to the loss of pigment so that they would be colorless or white.

I have tried to test these predictions by examining the British fauna as summarised by Thompson (1976) and Thompson and Brown (1984), supplemented by reports of burrowing opisthobranchs from elsewhere. First there are many burrowers that are as strongly pigmented as are surface living and epizootic forms. If color is fortuitous then some at least of these species should be deep burrowers which rarely come to the surface. Burrowing nudibranchs occur in the genera Armina, Cerberilla, Pseudovermis and possibly

Embletonia. There are no comprehensive descriptions of the burrowing and feeding habits of these animals, but *Cerberilla* (Aeolidacea) and *Armina* (Arminacea) feed on prey which projects from the substrate so there is presumably advantage in being camouflaged when feeding. Little is known of the habits of *Pseudovermis* and *Embletonia*, but *Pseudovermis* is a member of the interstitial fauna. These species lack pigment though the gut may be colored (brown or vermilion in *Embletonia*, depending on diet), and this is likely to improve camouflage when eating hydroids on the surface of the substrate.

Species of the Philinoglossacea also have some pigment (Thompson, 1976), but it is not known how deeply they burrow nor how often they live on the surface.

Pleurobranchaea spp. (Pleurobranchacea) also burrow, but in my experience they are normally only partly buried as they plough through sand; hence their colors can be interpreted as being cryptic.

In the Bullacea colored species occur in the genera *Bulla, Acteon, Haminoea, Atys, Roxania, Bullina, Micromelo, Hydatina, Runcina* and in the Aglajidae. However, species in the last four of these genera and in the Aglajidae spend much time on the surface instead of burrowing, so their coloration is likely to be cryptic or possibly aposematic. In the Runcinoidea for example, the European *Runcina coronata* (Quatrefages) is black and *R. ferruginea* Kress is red, while *R. katipoides* Miller and Rudman from New Zealand is striped. All three species appear to live on the surface of mud or algae and there is no record of their burrowing (Thompson, 1976; Rudman, 1971a). The other bullacean genera listed above include species which burrow. *Haminoea, Bulla* and *Quibulla* spp. plough through mud and sand secreting a mucous tube (Rudman, 1971a, b). Sand adhering to the mucus on the dorsal surface partially conceals the animal from above even though it may be crawling only a millimetre or two below the surface. However, these are all herbivores and are exposed to view when browsing on algae. *Haminoea hydatis* (L.) and *Roxania utriculus* (Brocchi) are also reported to swim (Thompson, 1976) where their coloration may be of protective value. The Acteonidae are carnivores typically feeding on polychaete worms (Hurst, 1965; Rudman, 1972a). *Acteon tornatilis* L. with a creamy white body and pink, mauve and white shell, burrows deeply but also comes to the surface from time to time (Fretter and Graham, 1954). Yonow (personal communication) records that it spends much time crawling on the surface of the sand at low tide. Although she reports that it is not particularly well camouflaged, there is probably selective advantage in being pink rather than white. *Pupa kirki* (Hutton) also burrows deeply but frequently returns to the surface and rests with its front end protruding (Rudman 1972a). In this position its drab color camouflages it.

The second group of burrowing opisthobranchs is either translucent or white to cream in color, but entirely lack colored pigment. Where a visible shell is present it is usually white or transparent. British species with these characters include *Diaphana minuta* Brown, *Retusa* spp., *Rhizorus acuminatus* Bruguière, *Cylichna cylindracea* (Pennant) and *Philine aperta* (L.). With the exception of *P. aperta* nothing appears to be known of whether these animals burrow deeply or shallowly, nor whether they frequently live on the surface. *P. aperta* can burrow deeply, but it also ploughs just below the surface where its white color is invisible because cilia and mucus carry a film of mud over its dorsal surface (Brown, 1934). It feeds on burrowing animals including the polychaete *Pectinaria* (Hurst, 1965). Two similar white philinids from New Zealand have also been studied, *Philine angasi* Crosse and Fischer and *P. auriformis* Suter (Rudman, 1972b). These both feed on burrowing bivalves, and *P. angasi* is apparently unable to swallow prey on the surface. Hence practically the entire life of these species is spent buried. Pigment can clearly have no protective value to them so the fact that they are white supports the hypothesis that conservation of energy is more important than any biochemical process which results in the formation of pigment as a biproduct. A possible exception to this conclusion is *Scaphander lignarius* (L.) which is yellowish and is thought to live and feed in a similar way to *Philine aperta* (Hurst, 1965). However, there is no good study of its burrowing habits. *Ringicula buccinea* (Brocchi), another white bullacean, has a large, thick external shell that is also white. It burrows just below the surface maintaining contact with the aerated water above by means of a short funnel (Fretter, 1960), but it is not clear how often it is exposed while burrowing.

Thus, although our knowledge of the ecology and behaviour of burrowing opisthobranchs is very superficial, the available evidence suggests that pigment in colored species is of protective value, that lack of pigment is a result of energy conservation in situations where color has no protective value, and that the occurrence of fortuitous colors in opisthobranchs remains unproven.

DISCUSSION

In this review I have tried to summarize the evidence concerning the functions of color in opisthobranch molluscs. There is a wealth of circumstantial evidence supporting the view that many species are cryptic or have specific resemblances to sessile prey, but there the hard evidence ends. There is tremendous scope for experimental (as opposed to anecdotal) study of the adaptive role of coloration in opisthobranchs. The subject of warning coloration requires thorough investigation using appropriate species of fish as predators, and the mimetic groups of nudibranchs pose a more formidable investigative problem. Are these müllerian or batesian or perhaps a mixture of the two with respect to different predators? Polymorphic species raise further questions: are these simply cryptic with polymorphism a defence against predators which hunt by acquiring search images of common prey (Edmunds, 1974)? Or are they aposematic in which case the role of polymorphism is obscure? Or are some morphs cryptic while others are aposematic? Experimental studies are also required on flash behavior, deimatic displays and deflective colors. Finally, on the question of fortuitous colors, I would like to suggest two areas that might repay further study. First, the observation that many burrowing and deep sea opisthobranchs are yellow rather than white requires

an explanation; and second, the detailed and often very intricate color pattern of many opisthobranchs raises the question of whether this level of detail is of functional significance.

ACKNOWLEDGMENTS

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